UPPER OLIGOCENE FOSSIL PUPAE AND LARVAE OF *CHAOBORUS TERTIARIUS* (VON HEYDEN) (CHAOBORIDAE, DIPTERA) FROM WEST GERMANY

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A redescription of Upper Oligocene fossil pupae of Chaoborus tertiarius *(von Heyden) and description of newly discovered fossil larval fragments suggests that speciation which led to ancestors of the sister subgenera,* Chaoborus s. str. *and* Schadonophasma *occurred 25 million years ago. Fossil larval mandibles may have come from a population ancestral to, or of, a sister species of* C. flavicans *within* Chaoborus s. str.

Une redescription des pupes fossiles de Chaoborus tertiarius *(von Heyden) datant de l'Oligocène supérieur et une description de fragments de larves récemment découverts suggèrent que le processus de spéciation qui a donné naissance aux ancêtres des sous-genres "seours"* Chaoborus s. str. *et* Schadonophasma *s'est produit il y a 25 millions d'années. Les mandibules des larves fossiles pourraient provenir d'une population ancestrale à, ou d'une espèce soeur de* C. flavicans *appartenant aux* Chaoborus s. str.

Fossils may provide data which permit testing of phylogenetic inferences based on less direct criteria. In addition, fossils exhibiting apomorphies that are used in determination of phyletic relationships of extant species, provide minimum ages for speciation events. During a systematic study of the species of the subgenus *Schadonophasma* Dyar and Shannon (Borkent, in press), I surveyed the literature for previous descriptions of fossils which may provide phylogenetic clues. Figures of fossil *Chaoborus* pupae by von Heyden (1862) exhibited one of the synapomorphies used to group the subgenera *Chaoborus s. str.* and *Schadonophasma.* I therefore undertook a study of the original material and I describe it more fully below. In addition, larval fragments were discovered which are also described. These results suggest that examination of other fossil chaoborid material (Edwards, 1923; Hennig, 1966; Hope, 1847; Loew, 1850, 1861; Meunier, 1902, 1904; Scudder, 1890 (questionable identification); Serres, 1829: 268), generally inadequately described, may be of use in providing information on the phylogeny of chaoborid species.

METHODS

The fossils were moistened with xylene and examined under both stereoscopic and compound microscopes. Larval fragments could only be seen when wet. Drawings were made by means of a drawing tube and, unless otherwise stated, scales on the figures represent one millimeter.

Chaoborus tertiarius (von Heyden)

Culcites tertiarius von Heyden 1862: 79. Two complete pupae, a series of disarticulated pupal parts, larval mandibles and anal fans on two pieces of brown paper coal. LECTOTYPE HERE DESIGNATED as complete male pupa (von Heyden 1862: Fig. 30). Labelled 'In 38802' '58787', 'Culicites tertiarius v. Heyden "abgebildetes originalex" Pal. XXXf. 30–35'. Upper Oligocene brown paper coal from Rott, Siebenbirge, West Germany. Material deposited in

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Chaoborus tertiarius Edwards 1923: 141.

Description. — Lectotype pupa: as shown in figure 1A; median ribs of pupal paddles darker than marginal ribs; median rib with apical bend; serrations at apex of outer pupal paddle ribs; width of abdominal segment VII/length of abdominal segment VII 1.33; pharate adult eye and abdominal setae evident.

Paralectotype pupae: as shown in figures 1B, C; 2A-H; reticulations visible on all pupal horns; median ribs of pupal paddles of all specimens darker than marginal ribs; serrations not visible at apex of outer paddle ribs; width of abdominal segment VII/ length of abdominal segment VII of complete pupa 1.57 (Fig. 1B); of third pupa with seventh abdominal segment 1.54 (Fig. 2A); complete pupa with projections which possibly are penis valves (Fig. 1C) and pharate adult setae evident.

Another pupal paddle, covered with glue, was not illustrated.

Paralectotype larvae: only mandibles (Fig. 3A–G), a pair of mandibles with a mandibular fan (Fig. 3H), and anal fans (Fig. 3I–L) present; mandibular fan with 14 bristles and anal fans with 18, 15, 14, and 14 setae. The mandibular fan bristles were identified as such by their placement near the pair of mandibles and by the presence in some of these of an apical bend also present in some mandibular fan bristles of extant species.

DISCUSSION

There seem to be two size classes (based on the length of the longest tooth) and types (based on the position of the subordinate tooth (st) – not visible in Fig. 3D–G) of mandibles as shown in figures 3A–F and figures 3G, H respectively. These may be of two instars of a single species or the mandibles of larvae of two distinct species. Because the placement of the subordinate tooth is constant between second, third and fourth instar larvae of extant *Chaoborus* species studied (Parma, 1971; pers. obs.), it seems more likely that two species are involved. However, it should be noted that the small subordinate tooth (Fig. 3A, B) in the intermediate position was very difficult to see and examination of further material may show these to be misinterpreted. If the subordinate tooth is truly intermediate, it would suggest that, because this feature is an autapomorphy of extant *C. flavicans* (Meigen), these mandibles are from larvae of a population either ancestral to extant *C. flavicans,* or of the sister species to that lineage.

The curvature of the median rib of the pupal paddle is a synapomorphy grouping *Chaoborus* species of the subgenera *Chaoborus s. str.* (which includes *C. flavicans*) and *Schadonophasma.* All fossil pupal paddles present exhibited this feature. As Edwards (1923) and Mägdefrau (1968) interpreted these fossils as Upper Oligocene in age, the speciation event resulting in the ancestors of the two subgenera must have occurred at least 25 million years ago.

The ratio of the width of abdominal segment VII/length of abdominal segment VII, although typical of extant species of *Chaoborus s. str.*, is probably a plesiomorphic condition within the species group *Chaoborus s. str.* plus *Schadonophasma* and therefore not indicative of phylogenetic relationships.

The complete paralectotype pupa possesses what possibly may be penis valves (Fig. 1C) which exhibit apical claws. Although similar to those of extant *C. trivittatus* (Loew) and *C. nyblaei* (Zetterstedt) in the subgenus *Schadonophasma* (Borkent, in press), the penis valves are also similar to those of *C. flavicans.* Therefore, until additional and better preserved material becomes available, these structures cannot yield any clues of phyletic relationships.

Statz (1944) briefly analyzed the ecological significance of *Chaoborus tertiarius* but discussed this in the context of generalizations concerning the genus. Subsequent investigations have shown that such generalizations are not entirely justified. *Chaoborus* species seem to be restricted to certain types of habitats and exhibit species specific behaviour (Borkent, in press).

The fossil material was in a remarkable state of presevation. The presence of two complete pupae, paired pupal respiratory horns, arranged setae of larval anal fans and a mandibular fan, and mandibles which were in pairs, indicates that these were preserved under conditions of extreme quiescence. Therefore, the habitat which these fossils occupied was probably a lake with an undisturbed bottom.

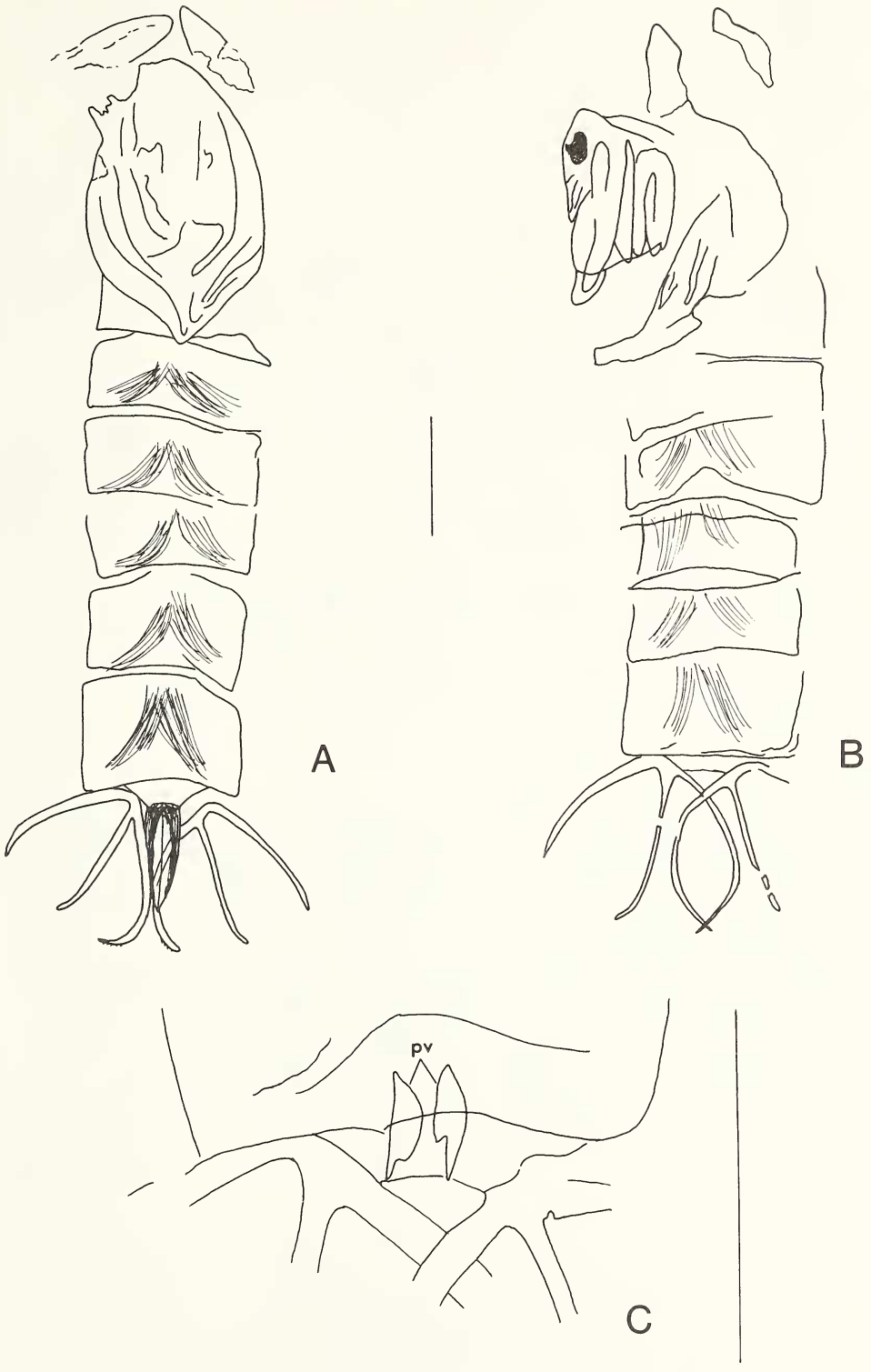

Fig. 1. Pupae of *Chaoborus tertiarius*. A. Lectotype, ventral aspect. B. Paralectotype, thorax in lateral aspect, abdomen in ventral aspect. C. Paralectotype, terminalia (pv = penis valves).

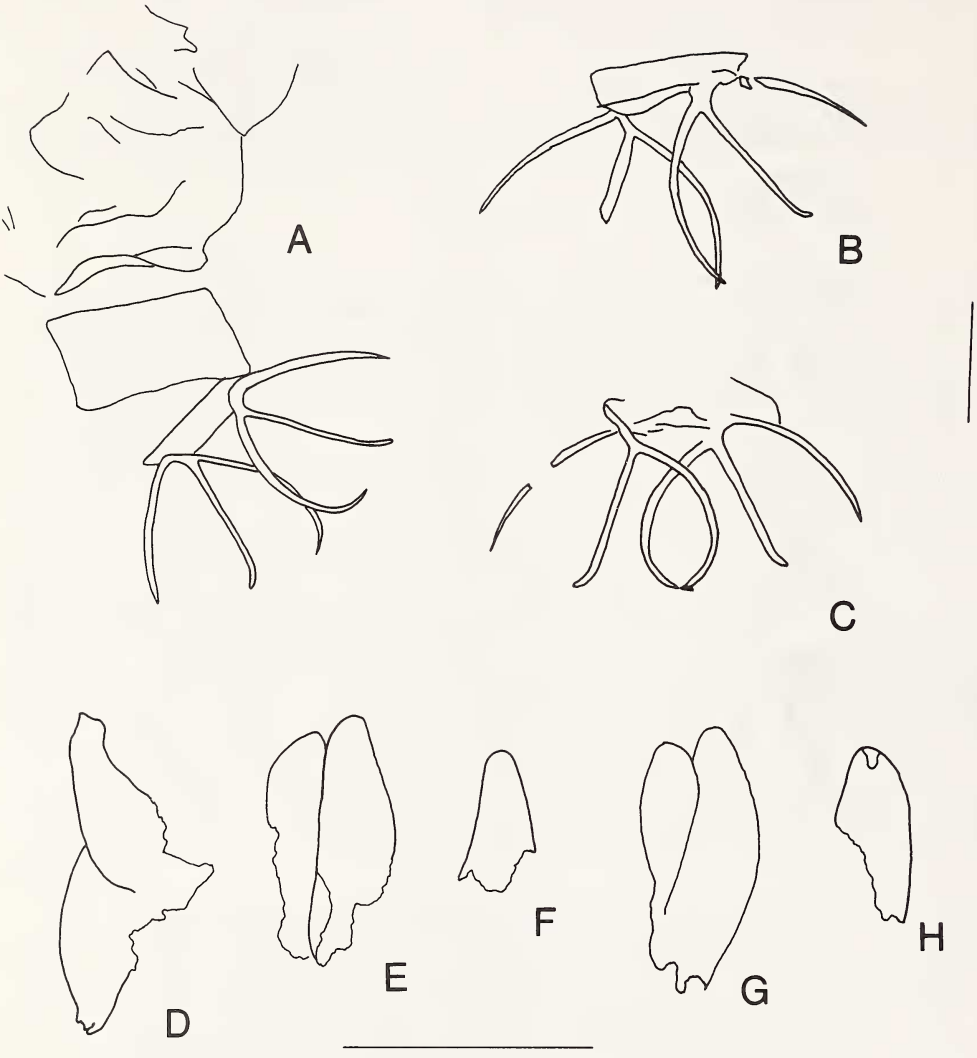

Fig. 2. Pupal paralectotypes. A–C. Paddles. D–H. Repiratory horns.

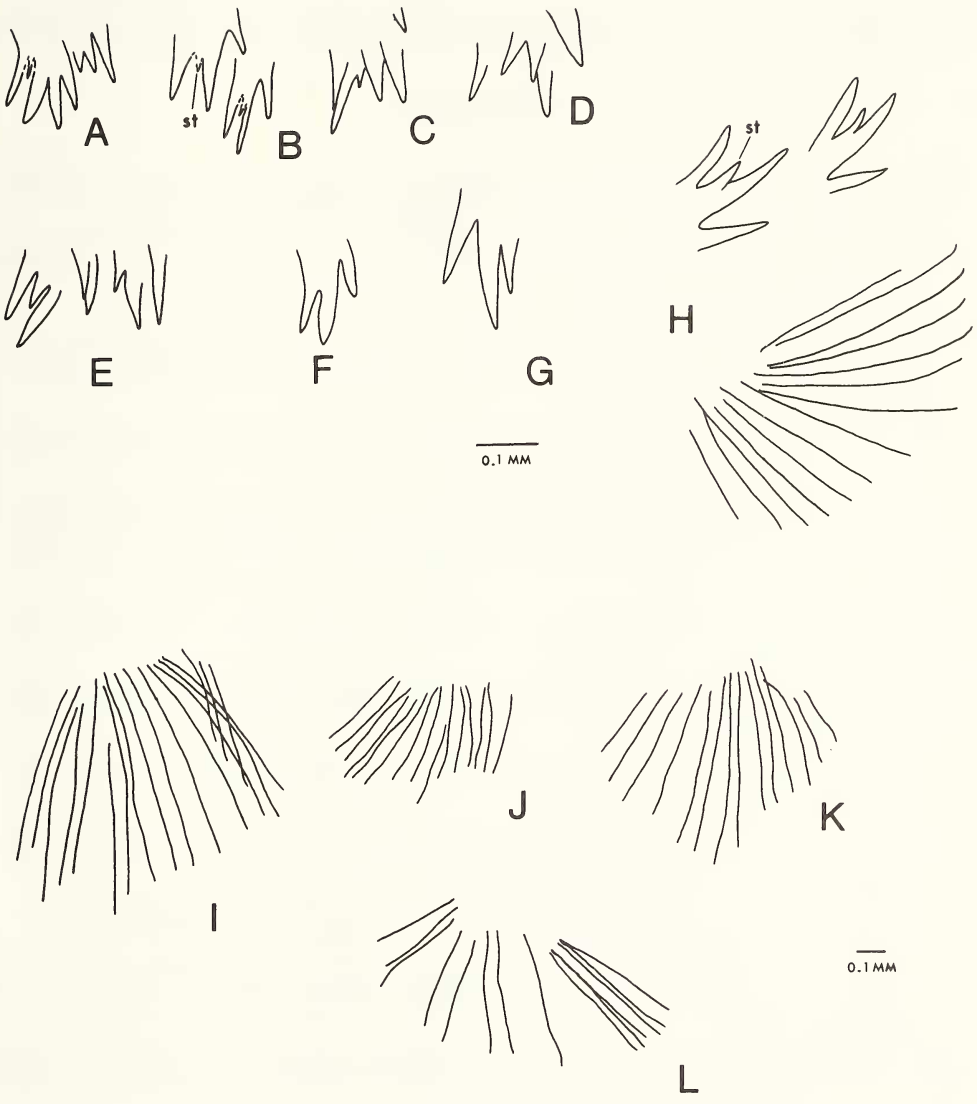

Fig. 3. Larval paralectotypes. A–H. Mandibles, H with mandibular fan. I–L. Anal fans. (st=subordinate tooth).

The concentration of fossils on two pieces of paper coal additionally suggests that the lake supported a large population of *Chaoborus tertiarius* although, as Statz (1944) discussed, it is puzzling why additional material has not been discovered.

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